THE NYSSACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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NYSSACEAE Dumortier, Anal. Fam. Pl. 13. 1829 (A. L. de Jussieu, Dict. Sci. Nat. **35**: 267. 1825, "Nysées"), nom. cons.

(TUPELO FAMILY)

Trees, mostly [polygamous or] androdioecious, with alternate, exstipulate leaves. Flowers small, ± regular, subtended by 1–5 bracts. Floral tube adnate to the ovary in bisexual or ♀ flowers; calyx lobes small or obsolete. Petals usually 5–10 [or absent]; stamens in ♂ flowers usually 10 or more in 2 ± distinct whorls around a nectariferous disc. Ovary inferior 1(rarely 2)-locular [or often 2-locular, or 6–8-locular], with 1 pendulous, apotropous ovule in each locule. Fruit a drupe; each locule of stone opening at apical part by a ± triangular abaxial valve at germination. Embryo straight; endosperm copious. (Cornaceae, in part, of many authors; including Davidiaceae H. L. Li.) TYPE GENUS: *Nyssa* L.

Three genera and seven or eight species, distributed in eastern Asia and eastern North America, mostly in warm-temperate areas. *Camptotheca* Decaisne and *Davidia* Baillon are monotypic genera of China, while *Nyssa* is eastern American-eastern Asian in distribution.

Harms treated *Camptotheca* and *Nyssa* as subfam. Nyssoideae and *Davidia* alone as subfam. Davidioideae of the Cornaceae. Wangerin retained these as the two subfamilies of a separate family, Nyssaceae. A close relationship between Cornaceae and Nyssaceae, supported by evi-

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Preserved flowers and fruits were obtained with the aid of Mr. W. W. McNeil, Superintendent, Seashore Natural Area, Virginia Beach, Virginia; Mr. Gurdon L. Tarbox, Jr., Director, Brookgreen Gardens, Murrells Inlet, South Carolina; Prof. Elso S. Barghoorn, Harvard University; and Prof. R. B. Channell, Vanderbilt University. Dr. Wood gave generously of his time and experience to assist me in revising and condensing my earlier publications for this article. I thank Prof. Robert F. Thorne, Rancho Santa Ana Botanic Garden, for his thoughts on the infraspecific variants of *Nyssa sylvatica*. The drawings illustrating *Nyssa* were made by Arnold D. Clapman under the supervision of Dr. Wood.

dence from palynology, floral and wood anatomy, serology, and cytology, has not been challenged in recent years; however, the Nyssaceae are here tentatively treated as a separate family because of their greater number of petals and stamens and their unique triangular germination valves.

The chromosome number of *Davidia* has been reported as $2n = \pm 40$ and that of *Nyssa sylvatica* as $2n = 44$. The latter count may provide further evidence that Cornaceae and Nyssaceae are related, since $2n = 22$ for most species of *Cornus*.

Considering the present small size of the group and its rather limited modern distribution, the Nyssaceae have one of the most remarkable fossil records of all angiosperm families. Excellently preserved fruits have been found in England, continental Europe, Siberia, Japan, and the western United States; nyssaceous pollen is a frequently encountered microfossil in continental deposits of Tertiary age throughout the Northern Hemisphere; and leaf impressions resembling foliage of *Nyssa* are often found in association with the pollen and fruits. Moreover, silicified woods from Japan and from the state of Washington and a lignitized wood from the Netherlands have been assigned to the family. Fossil Nyssaceae are common in all major time zones from the Eocene through the Pliocene; the present restricted distribution of the family is clearly a relatively recent phenomenon connected with Pleistocene glaciation.

Comparative floral anatomy of modern Nyssaceae indicates that in ancestral members the floral parts were more numerous, and this is nicely confirmed by fossils. Many of the oldest fruits are three- or four-carpellate, and vestiges of major vascular bundles provide evidence for the greater number of petals and stamens in these extinct forms. Some of the ancient fruits are also much larger than their present-day counterparts. The affinities of certain fossils from North America are with modern Asiatic Nyssaceae.

Aside from *Nyssa*, only *Davidia involucrata* Baill., dove tree, cultivated to a limited extent for its showy, bracteate inflorescences, is of any economic importance.

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1. **Nyssa** Linnaeus, Sp. Pl. 2: 1058. 1753; Gen. Pl. ed. 5. 1028. 1754.

Deciduous trees, becoming shrubby under adverse conditions of growth; branching markedly excurrent; bark gray, divided into segments by deep fissures; base of trunk enlarged and roots sometimes forming arches when growing in water. Leaves alternate, often crowded near ends of branches, simple, petiolate, exstipulate; blade membranaceous or subcoriaceous, elliptic or ovate to narrowly or broadly obovate, entire (or irregularly dentate, especially on seedlings and on sprouts arising from roots). Inflorescences (or solitary flowers) axillary, pedunculate, produced with the leaves from mixed imbricate buds. Staminate flowers in short racemes or heads; calyx lobes minute; petals 5–10; stamens 8–15, much longer than petals, usually in 2 ± distinct whorls, the outer whorl antipetalous, the

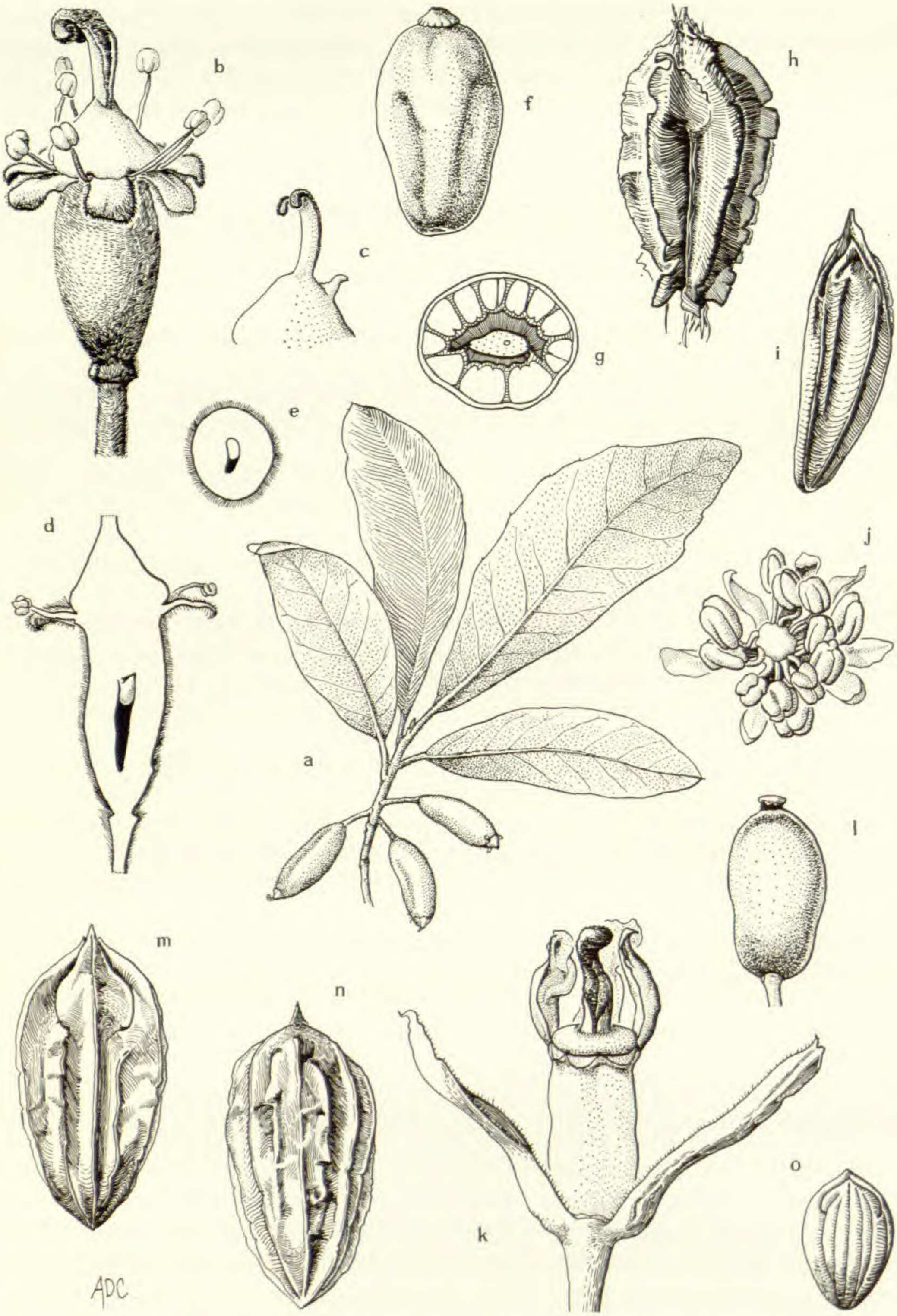

FIG. 1. **Nyssa.** a–i, *N. ogeche*: a, branchlet with immature fruit, × 1/2; b, functionally unisexual flower — note scars of fallen bracts at base of ovary, × 4; c, disc and style with rudimentary second style, × 4; d, flower in diagrammatic vertical section to show locule and ovule, × 4; e, diagrammatic cross section of ovary and ovule, × 4; f, mature fruit, abaxial surface, × 1; g, immature fruit from "a" in diagrammatic cross section to show radicle of embryo, endosperm

inner alternipetalous; anthers on short, green, filiform filaments, introrse, longitudinally dehiscent, basifixed; pollen tricolporate; gynoecium absent, except for occasional presence of stylar rudiment at center of pulvinate disc. Bisexual, ♂-sterile, or ♀ flowers solitary or in inflorescences of 2–4 [or more] and sessile (in ours) on slender peduncles; floral tube urceolate or campanulate, densely tomentose to glabrous, adnate to the ovary; calyx lobes, when present, usually 5; petals 5–8, tomentose or glabrous, ovate or oblong; stamens often visibly abortive, fewer than in ♂ flowers or lacking, about equal in length to petals; nectariferous disc pulvinate or conical; gynoecium syncarpous, 1(rarely 2)-carpellate; style 1 (rarely 2, more often with only the rudiment of a second style); stigma reflexed or revolute, abaxially sulcate; ovary inferior, adnate to floral tube and disc, usually 1-locular (or 2-locular when 2 styles are present) and pseudomonomeric, with 1 apotropous, 1-integumented ovule pendent from the axile placenta near apex of (each) locule. Drupe ovoid or ellipsoid, blue-black, purple, or red, with corky epidermal spots, crowned by the persistent disc; outer tissues fleshy; woody endocarp ovate, obovate, or elliptic in outline, sometimes flattened abaxially, bearing broad longitudinal ridges, sharp ridges, or papery wings. Seed conforming to locule; seed coat membranaceous. TYPE SPECIES: *N. aquatica* L. emend. Du Roi; see Eyde, Taxon 13: 129. 1964. (*Nyssa* or *Nysa*, the name of a nymph, applied by Linnaeus in the belief that all members of the genus are aquatic; cf. *Hortus Cliffortianus* 462. 1738.) — TUPELO, GUM.

Three or four species in North America and two in southeastern Asia.

Nyssa sylvatica Marsh. var. *sylvatica* (including vars. *dilatata* Fern. and *caroliniana* (Poir.) Fern.), black gum, sour gum, or pepperidge, $2n = 44$, is a common constituent of moist forests from Maine to southern Florida, west to Texas (Brazos River), Oklahoma, eastern Kansas, Illinois, and Michigan, with disjunct Mexican stations in Hidalgo, Puebla, and Chiapas. A tree frequently 20 m. tall (occasionally more than 25 m.), it is characterized by entire-margined obovate to elliptic leaves; pediceled staminate flowers; two, three, or four fertile flowers on each peduncle; blue-black ovoid (to globular) drupes 1–1.5 cm. long with five distinct calyx lobes; and stones with low, rounded ridges. The var. *biflora* (Walt.) Sarg. (including *N. ursina* Small), swamp black-gum, $2n$ = ca. 44, differs in its narrower leaves more gradually tapered at base, shorter fruiting peduncles, and a predominance of paired fertile flowers (although one or three may occur). It is largely confined to very wet soils or standing water in swamps

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(stippled), developing endocarp (note germination valve, cf. "i"), and papery wings in mesocarp, × 2; h, mature stone with papery wings — note vascular bundle between wings, × 2; i, same, wings removed, abaxial surface with germination valve, × 2. j–n, *N. aquatica*: j, staminate flower seen from above, showing petals, stamens, and disc, × 4; k, carpellate flower before anthesis, stigma and style not fully developed, three petals removed, × 4; l, mature fruit, × 1; m, stone, abaxial surface, showing germination valve, × 2; n, same, adaxial surface, × 2. o, *N. sylvatica*: stone, abaxial surface, showing germination valve, × 2.

of the Coastal Plain from eastern Texas to eastern Virginia. This variant is treated as a species, *N. biflora* Walt., by some authors, but the morphological differences that separate it from var. *sylvatica* are not as great as those that distinguish undisputed species of *Nyssa*, and plants are found that are intermediate in character between the two taxa. Since var. *biflora* can be roughly delimited ecologically, geographically, and morphologically, some authors may prefer to treat it as a subspecies.

The closest relative of *Nyssa sylvatica* is *N. sinensis* Oliver, of mesophytic forests in southern China and Burma. *Nyssa sinensis* is notable for having pediceled fertile flowers borne mostly four in a cluster and in commonly having two styles and a bilocular ovary. Of the two, *N. sinensis* is morphologically more primitive and somewhat less winter hardy. Fossil materials show that the subgeneric stock which gave rise to this pair of species has been in existence since early Tertiary times and that it was distributed around the Northern Hemisphere before the Pleistocene glaciation.

Although bearing no close relationship either to each other or to the *Nyssa sylvatica* alliance, *N. aquatica* L. and *N. ogeche* Bartr. ex Marsh. share in common capitate staminate inflorescences, solitary fertile flowers with obsolete calyx lobes, and drupes longer than 2 cm. *Nyssa aquatica* has leaves with coarse, irregularly distributed mucronate teeth; purple, oblong drupes with the floral tube constricted below the flat disc; and mucronate stones with eight to ten sharp longitudinal ridges. It is common in backwaters of the Mississippi Embayment and Gulf and Atlantic coastal plains, reaching its limits in southern Illinois, eastern Texas, northern Florida, and southeastern Virginia. In contrast, *N. ogeche* (including *N. acuminata* Small) has leaves with variable margins; hairy-peduncled red drupes without a constriction beneath the conical disc; and sharp-pointed stones with about 12 ridges, their crests extended as wide, papery wings. Reaching only about 10 m. (*vs.* 33 m. in *N. aquatica*), it grows only in swamps of southern Alabama, northern Florida, southern Georgia, and southernmost South Carolina. Anatomical features of the fruit suggest an affinity between *N. aquatica* and *N. javanica* (Blume) Wangerin, of southeastern Asia.

Locally, some nyssas develop a shrubby form when subjected to adverse growing conditions, such as periodic burning; the segregation of these forms as separate species (*Nyssa acuminata*, *N. ursina*) seems unsupportable.

The tolerance of *Nyssa* species for saturated soil and standing water is remarkable. Of our species, only *N. sylvatica* var. *sylvatica* is found in upland situations; the others are characteristic of deep fresh-water swamps, where they occur in dense stands, with *Taxodium* the most frequent associate. The genus contributes a substantial proportion to the pollen-rain in fresh-water swamps; it is not surprising, therefore, that *Nyssa* is an important entity in palynological studies of fresh-water peats and brown coals. It is clear that many extinct species of the genus occupied aquatic habitats like their modern counterparts. Some of the

brown coals that have yielded nyssaceous pollen and fruits originated as long ago as the Eocene epoch. Although aquatic nyssas can grow in sites where water rises annually to depths of five feet or more and seeds can remain viable after months of submergence, periodic drought is required for germination and perpetuation of the species. Fruits float well, and water currents undoubtedly play a major role in distributing the aquatic species. The fruits of *N. sylvatica*, on the other hand, are relished by birds, which apparently aid in maintaining the wider distribution of this species.

Pollination is by insects, but Wodehouse reports the collection of air-borne pollen about 150 m. from a tree of *Nyssa sylvatica* var. *sylvatica*.

The leaves of *Nyssa sylvatica* var. *biflora* have the capacity for accumulating unusually large amounts of cobalt, a phenomenon which has been used in evaluating the cobalt status of soils.

In the United States, *Nyssa* species annually provide more than 200 million board feet of lumber. Although a tendency to warp because of interlocking grain makes the wood unsuitable for many purposes, it is used extensively for boxes and crates, as well as for furniture, flooring, and paper pulp. The light wood from roots and stumps of *N. aquatica* was formerly used for floats and for a kind of surgical sponge called "tupelo tent." *Nyssa sylvatica* is cultivated for its colorful autumn foliage. Plantings of *N. ogeche* have been undertaken in western Florida in an effort to increase the production of the highly regarded tupelo honey; fruits of this species can be made into a preserve, "ogeechee limes."

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